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# Ecosystem type and resource quality are more important than global change drivers in regulating early stages of litter decomposition

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ABSTRACT

Litter decomposition is fundamental for nutrient and carbon (C) cycling, playing a major role in regulating the Earth's climate system. Climate change and fertilization are expected to largely shift litter decomposition rates in terrestrial ecosystems, however, studies contextualizing the relative importance of these major global change drivers versus other key decomposition drivers such as substrate quality and ecosystem type are lacking. Herein, we used two independent field experiments in an Eastern Australian grassland (Experiment 1) and a forest (Experiment 2) to evaluate the role of (i) litter quality, (ii) nutrient addition (N, P and K in full factorial combination; Experiment 1), and (iii) a combination of N addition and irrigation (Experiment 2) in litter decomposition, substrate-induced respiration and microbial abundance. Regardless of experimental treatments, forest soils decomposed litter between 2 and 5 times faster than grassland soils. This was principally controlled by the greater ability of forest microbes to respire C-based substrates and, ultimately, by soil N availability. The experimental treatments accounted for only relatively small differences in our measured variables, ranging from 10 to 15% in the case of the irrigation-by-N-addition forest experiment to almost negligible in most of the grassland nutrient addition plots. In the latter experiment, decomposition and soil activity responses were associated with either K addition or interactions between K and other nutrients, suggesting a key role for this often-neglected soil nutrient in controlling litter decomposition. Our study provides evidence that while nutrient enrichment and/or irrigation have the potential to affect litter decomposition rates in grassland and forest ecosystems, land use change that results in loss or gain of forested area is likely to exert a much greater impact than these other two drivers.

## 1. Introduction

Litter decomposition is fundamental for nutrient and carbon (C) cycling, affecting plant productivity, species composition and long-term C storage (Bradford et al., 2016), ultimately playing a major role in regulating the Earth's climate system (Bonan et al., 2013; Chapin et al., 2009). Litter decomposition is mainly controlled by resource quality, soil properties and climate (via soil temperature and moisture; Anderson, 1991; Walter et al., 2013; Bradford et al., 2016). The capacity of a soil to decompose plant litter is also substantially controlled by the abundance, composition (e.g., fungi:bacteria ratio) and activity of soil microbial communities and by soil microbe-plant interactions (e.g., via release of different types and amounts of rhizodeposits; Leff et al., 2015; Philippot et al., 2013; Prober et al., 2015). For example, fungi decompose low quality litter and recalcitrant organic compounds more efficiently than bacteria (van der Wal et al., 2013) and are thus associated with lower fertility and drier soil conditions (Schwinning and Sala, 2004). On the other hand, soil bacteria tend to thrive in nutrient-rich environments where more labile organic matter inputs dominate (Fierer et al., 2012).

Litter decomposition is currently being affected by multiple global change drivers, including human-induced climate change, over-use of fertilisers and land use change (Conant et al., 2001; Knorr et al., 2005; Walter et al., 2013). Increases in soil nutrient availability due to fertilization or atmospheric deposition (Fowler et al., 2013; Gruber and Galloway, 2008) can influence the capacity of an ecosystem to

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decompose litter both via changes in plant chemistry that, in turn, influence the quality and decomposability of litter inputs and via interactions with soil microbial communities (He and Dijkstra, 2014; Xia and Wan, 2008). In this sense, Cleveland et al. (2014) showed that 64% of the variation in decomposition rates in a multi-site study was explained by litter quality, with a further 25% explained by the type of soil microbial inoculum. Since soil moisture is a strong determinant of microbial activity (Schwinning and Sala, 2004), changes in water availability associated with predicted climate change can also be expected to influence litter decomposition (García-Palacios et al., 2013). Direct effects of drought are frequently associated with a reduction of decomposition rates due to inhibitory effects on microbial activity and biomass (Sanaullah et al., 2012; Walter et al., 2013), whereas an increase in precipitation typically results in enhanced microbial activity and nutrient immobilisation (Sponseller, 2007), which, in turn, results in greater decomposition (Djukic et al., 2018). Identifying the roles of land-use transformation, climate change and fertilizer application in regulating organic matter turnover is important given the cascading consequences that such changes imply for the functioning of ecosystems and the goods and services they provide (Allison et al., 2013; Britton and Fisher, 2010; Fay et al., 2015; Stevens et al., 2004; Wang et al., 2015; Wilcox et al., 2015; Zechmeister-Boltenstern et al., 2015).

Investigating the role of nutrients other than N, such as phosphorus (P), potassium (K) and trace elements, as modulators of litter decomposition is equally relevant, as many terrestrial ecosystems are now shifting to P- rather than N-limitation under sustained increases in atmospheric N deposition (Oheimb et al., 2010; Sardans et al., 2012; Vitousek et al., 2010). This is especially true for many southern-hemisphere ecosystems such as those from Australia, largely known for their highly-weathered, P-poor soils (Lambers et al., 2015). Understanding the limiting role of nutrients for litter decomposition rates is of particular importance in the context of climate change, as a more efficient C processing and stabilisation could negatively feedback with climate change (O'Mara, 2012; Reich et al., 2006). Moreover, given that mineralization of fresh litter in the early stages (days to weeks) of the decomposition process is responsible for one of the greatest $CO_2$ fluxes at the global scale (Djukic et al., 2018; Rinkes et al., 2014), understanding how land use change, climate change and the availability of essential macro and micronutrients control early-stage litter decomposition is crucial to inform Earth System Models (Bonan et al., 2013).

Herein, we used two independent field experiments and three different litter types to evaluate the role of litter quality (labile, intermediate and recalcitrant) in regulating the early stages (0–60 days) of decomposition rates in: (i) a grassland under nutrient addition (N, P and K in full factorial combination; Experiment 1) and (ii) a forest under a combination of N addition and irrigation (Experiment 2). To simulate different litter qualities, we used two standard litter substrates (commercially obtained green tea and black tea) and locally collected, oven-dried plant material from a grassland nearby (Power et al., 2016). Experiment 1 was carried out in a former pasture grassland that is part of the Nutrient Network research cooperative (https://nutnet.org/), whereas Experiment 2 was undertaken in a blue gum (*Eucalyptus saligna*) plantation at the Hawkesbury Forest Experiment (hereafter, HFE site). Both sites are located approximately 100 m from each other within the HFE experimental facility of Western Sydney University in Richmond, Eastern Australia.

We specifically sought to evaluate the relative importance of three major global change drivers (fertilization, water availability and land-use conversion) versus key local drivers (microbial abundance, metabolic profile of microbial communities, litter quality and soil properties) in controlling plant litter decomposition in two adjacent ecosystems from Eastern Australia subjected to different management regimes. We hypothesize that: (1) Increases in nutrient and/or water availability will not increase decomposition rates of recalcitrant litter, despite significant increases in labile litter decomposition associated with nutrient addition and irrigation; (2) the effects of irrigation and nutrient addition will be consistently smaller than the variations associated with the ecosystem type; in particular, we hypothesize that litter decomposition rates will be greater at the forest than at the grassland site given that forests typically store a greater amount of organic matter than grasslands, a factor that is associated with faster litter decomposition rates (Zhang et al., 2008). By answering these fundamental questions, we will contribute a more mechanistic understanding of potential interactions between ecosystem type, the quality of litter inputs, C sequestration and global environmental change drivers. We will also provide novel insights into the importance of fertilization and climate change in driving future responses of litter decomposition in ecosystems from eastern Australia.

## 2. Methods

### 2.1. Study sites

The sites chosen for this study belong to the Western Sydney University, in the Sydney basin, at Richmond, New South Wales, Australia (33° 24′S, 150° 59′E). The mean annual temperature in Richmond is 17 °C, and the average annual precipitation is 801 mm, with a precipitation/evapotranspiration ratio of 0.6, classifying it as a dry subhumid environment under UNEP classification (Millennium Ecosystem Assessment, 2005).

### 2.2. Nutrient Network site (experiment 1 - NPK addition)

Soils at this site belong to the Clarendon sand series (i.e., coarse sand brownish grey to a depth of ~75 cm overlying light grey and yellow brown sandy clay) and are characterized by low organic matter content (2.2%) and low pH (~5). The experiment was set up in 2013 and received the first fertilizer application in April 2014. The experiment consists of eight treatments (N, P and K in full factorial combination) and four replicate plots per treatment, giving a total of thirty-two plots arranged in a 4-block design. Nutrients have been added annually, at a rate of 10 g N $m^{-2}$ $yr^{-1}$ as timed-release urea, 10 g P $m^{-2}$ $yr^{-1}$ as triple-super phosphate and 10 g K $m^{-2}$ $yr^{-1}$ as potassium sulphate following the standard protocol of the Nutrient Network (Borer et al., 2014). A single application of 100 g $m^{-2}$ $yr^{-1}$ of a micronutrient mix (6% Ca, 3% Mg, 12% S, 0.1% B, 1% Cu, 17% Fe, 2.5% Mn, 0.05% Mo, and 1% Zn) was applied once, in 2014.

### 2.3. Hawkesbury Forest Experiment (HFE) site (experiment 2 - irrigation x fertilization)

Soils at the HFE are sandy loams and are also characterized by low organic matter content (Barton et al., 2010). The fertilization by irrigation experiment started in 2007 and includes four treatments: control, irrigation, N fertilization, and irrigation plus N fertilization. Each treatment is replicated four times in a randomized block design, with individual treatment plots measuring 38.5 × 41.6 m. *Eucalyptus saligna* Sm. seedlings were planted in April 2007. Trees were initially supplied with 50 g of $(NH_4)_2PO_3$ starter blend (N 15.3%, P 8.0%, K 16.0%, S 7.7% and Ca 0.3%) per plant to aid with seedling establishment. The fertilization treatment started in January 2008 as a solid N fertilizer (N 20.6%, P 3.0%, K 7.5%, S 3.8%, Ca 4.4%) at a rate of 25 kg N $ha^{-1}$ $year^{-1}$. Since October 2008, solid N fertilizer (N 21.6%, P 8.1%, K 12.0%, S 0.6%) has been added at a rate of 150 kg N $ha^{-1}$ $year^{-1}$. In the irrigation treatment, water is added at a rate of 15 mm every 4 days from September to April (the Austral spring and summer), and 7–10 mm every 4 days from May to August (irrigated plots received c. 1000 mm $year^{-1}$ in addition to ambient rainfall). The irrigation plus fertilization treatment started in October 2008, with the addition of a complete liquid fertilizer at a rate of 150 kg N $ha^{-1}$ $year^{-1}$. The total amount of water added to the irrigated plus fertilization treatment was the same as in the irrigated-only ones. More detail on the experimental

design can be found in Hu et al. (2015).

### 2.4. Litterbags

To make the litterbags, we used two different types of commercial tea as standard substrates (Lipton® black and green tea), in addition to oven-dried (60 °C) local green plant material collected from a grassland near the study area (~300 m away). The dominant species in these local litter were predominantly C4 and C3 grasses, including *Cynodon dactylon* (L.) Pers., *Eragrostis brownii* (Kunth) Nees., *Paspalum notatum* Flüggé), *Lolium perenne* L. and *Microlaena stipoides* (Labill.) (R.Br.). Forbs were also present in lower abundances, including *Hypochaeris radicata* L. and *Plantago lanceolata* L. Despite not being a realistic representation of local litter types, these three contrasting substrates were chosen to represent a well-defined substrate quality gradient, with black tea being the most oxidised and recalcitrant form and green tea the most labile one. This *a priori* decomposability gradient was confirmed in our study by several metrics (see Results section below). Litterbags (5 × 5 cm) were constructed using nylon fabric (250 μm mesh) and filled with 2 g of dry material. Litterbags were buried (8 cm depth) at both sites in December 2014 (early summer) and left to decompose in the field for 60 days. After this period, bags were retrieved, cleaned, oven-dried at 60 °C, and then weighed.

### 2.5. Soil sampling and processing

Soil samples (0–10 cm) were collected in paralell with litter bag deployment using an auger (5 cm width). Soil samples were taken to the lab and refrigerated (4 °C) until processed (within two weeks for nutrient determinations and MicroResp® analyses). A small portion of soil was also immediately frozen for molecular analyses (quantitative polymerase chain reaction; qPCR) and another fraction weighed and oven-dried at 70 °C for three days to determine the volumetric soil water content (%).

### 2.6. Extractable C and N determinations

Four grams of fresh soil (un-sieved, but with stones and large organic debris removed) was shaken with 20 ml 0.5 M $K_2SO_4$ at 160 rpm for 1 h. Samples were then filtered (Whatman® quantitative filter paper, ashless, Grade 42) and frozen until total extractable C and N analyses were done with a total organic C analyzer (TOC-L CPH/CPN, Shimadzu Scientific Instruments, Rydalmere, NSW, Australia) following the methods described in Hasegawa et al. (2016).

### 2.7. qPCR

Soil DNA was extracted from 0.5 g of defrosted soil using the Powersoil® kit (Mo Bio Laboratories, Carlsbad, CA, USA). The extracted DNA was then used for downstream analysis to evaluate the total and relative abundance of fungi, bacteria, archaeal nitrifiers (AOA) and bacterial nitrifiers (AOB) by means of qPCR. QPCR reactions were carried out on an ABI 7300 Real-Time PCR (Applied Biosystems, Foster City, CA, USA). The bacterial 16S-rRNA genes and fungal internal transcribed spacer (ITS) were amplified with the Eub 338-Eub 518 and ITS 1-5.8S primer sets (Evans and Wallenstein, 2012).

### 2.8. MicroResp assays

MicroResp® substrate-induced respiration (SIR) assays were carried out following manufacturer's instructions using several C sources (oxalic acid, glucose, cellulose and lignin) representing a gradient of decreasing substrate degradability. In addition, we infused litterbags like the ones buried in the field containing black tea, green tea and local litter for 5 min in boiling water and used the resulting infusion as additional substrates in the MicroResp® assays, giving a total of seven substrates.

### 2.9. Statistical analyses

All statistical analyses were carried out using R version 3.4.0 (R Core Team, 2017). Using linear mixed effects models (*lme* function of the 'nmle' package), we first evaluated the relative importance of "litter type" (litterbags) "C substrate" (MicroResp® assays) and experimental treatment (NPK addition [Experiment 1] or N fertilization and irrigation [Experiment 2]) on litter mass loss, substrate induced respiration rates, and bacterial and fungal abundance. Analyses were conducted separately for each experiment. In all cases, "litter type" or "C substrate" were nested within plots. We then used all replicates (n = 48) to carry out linear and non-linear regression analyses between SIR rates, microbial abundance and litter decomposition.

After this, we used structural equation modelling (SEM; Grace, 2006) to achieve a system-level understanding on the role of ecosystem type, manipulated drivers and environmental factors in controlling litter decomposition. In this model, N fertilization (dummy variable coded as: 0 = control and 1 = N addition) and ecosystem type (dummy variable coded as: 0 = grassland and 1 = forest) were considered as exogenous variables that influenced all the response variables considered but that were independent from each other. Fungal and bacterial abundance were predicted to determine the ability of soils to respire labile (oxalic acid), intermediate (infused tea and litter substrates) and recalcitrant (lignin) C-based substrates, whereas the ability of soils to respire different substrates determined the availability of soil N. Microbial abundance, substrate respiration capacity and soil N availability were all predicted to influence litter decomposition. In this analysis, we used all replicates (n = 48) but did not consider effects associated with drivers that were not replicated across the two sites (i.e., irrigation and fertilization with P and K + micronutrients). Thus, a certain degree of unexplained variability associated with these factors is expected. SEMs were carried out using the *sem* function from the 'lavaan' package.

## 3. Results

### 3.1. Nutrient Network site (experiment 1)

Litter quality was, by far, the main factor regulating decomposition rates at the grassland site (Experiment 1). In agreement with our initial predictions, green tea (labile litter) and local litter were the more rapidly decomposed by the local microbial community, compared to black tea (i.e., recalcitrant litter; $P < 0.001$; Fig. 1a; Table 1). There were very few effects of nutrient treatment on litter decomposition during the two months of field incubation, with only a marginally significant N:P:K interaction ($P = 0.06$) associated with a slightly greater mass loss under simultaneous addition of NPK (Fig. 1a). Substrate type was also the main predictor of SIR rates (Table 2), again with glucose and oxalic acid being the more easily respired substrates (Fig. 1c). Potassium addition marginally increased SIR rates ($P = 0.06$; Table 1), particularly in the case of black tea ($P = 0.05$; Table 3), cellulose ($P = 0.08$; Table 3) and local litter ($P = 0.08$; Fig. 1; Table 3), while there were significant N:K and P:K interactions for the rates of oxalic acid-induced ($P = 0.01$; Table 3) and cellulose-induced ($P = 0.04$; Table 3) respiration, respectively. Black tea-induced and green tea-induced respiration rates showed a pattern very similar to oxalic acid, whereas respiration rates associated with local litter were more similar to lignin and cellulose. The microbial community had a greater abundance of bacteria than fungi but there were no significant effects of nutrient addition on overall microbial abundance nor on the abundance of any microbial group, despite all fertilization treatments having generally greater fungal abundance (Fig. 1). The ratio between archaeal and bacterial nitrifiers (AOA:AOB ratio) was interactively affected by N:P additions, with the combined addition of N + P being

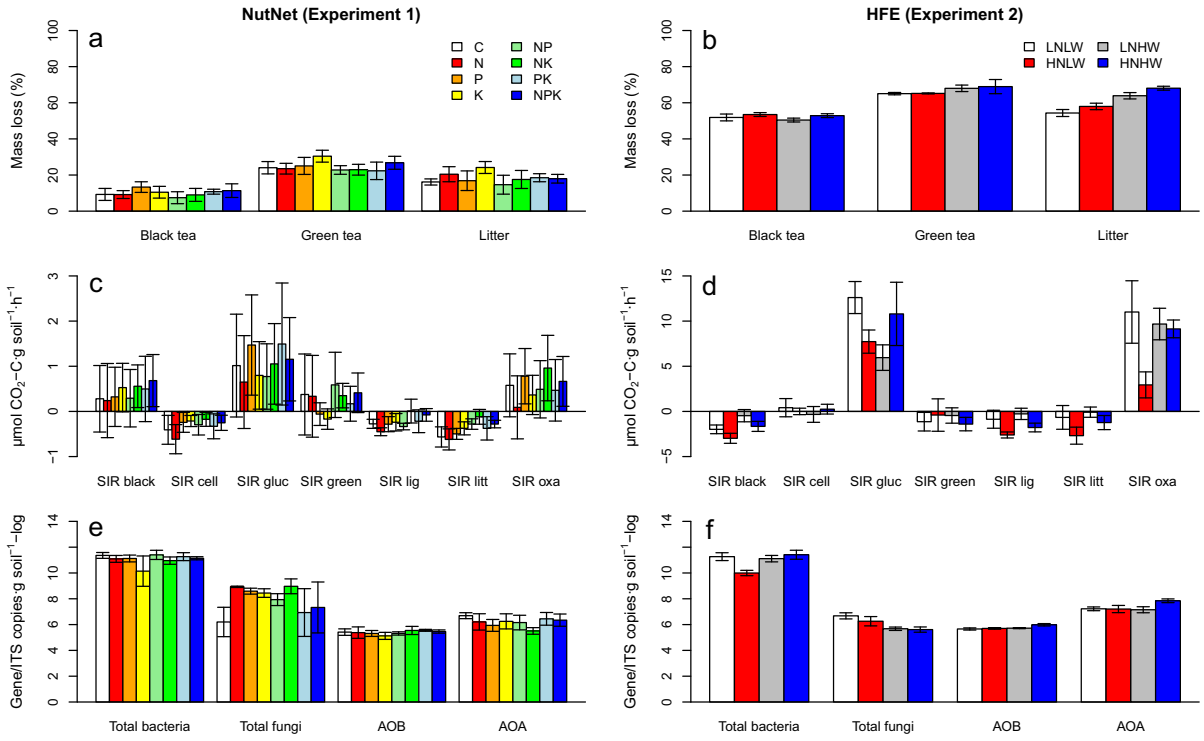


**Fig. 1.** Litter decomposition, substrate-induced respiration rates and microbial abundance (log-transformed) in response to nutrient addition (NutNet, Experiment 1; left-hand side panels) and N addition plus irrigation (HFE, Experiment 2; right-hand side panels). LNLW = low-N, low-water, HNLW = high-N, high-water, LNHW = low-N, high-water, HNHW = high-N, high-water. SIR = substrate-induced respiration rates. Black = infused black tea, cell = cellulose, gluc = glucose, green = infused green tea, lig = lignin, litt = infused litter, oxa = oxalic acid. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 1**
Litter type and treatment effects on litter decomposition after 60 days at the NutNet (Experiment 1) and HFE (Experiment 2) sites.

| NutNet | numDF | denDF | F-value | *P*-value |
|---|---|---|---|---|
| N | 1 | 21 | 1.09 | 0.31 |
| P | 1 | 21 | 0.30 | 0.59 |
| K | 1 | 21 | 1.32 | 0.26 |
| Litter type | 2 | 48 | 57.52 | **0.00** |
| N x P | 1 | 21 | 0.13 | 0.73 |
| N x K | 1 | 21 | 0.07 | 0.80 |
| P x K | 1 | 21 | 0.07 | 0.80 |
| N x Litter type | 2 | 48 | 0.01 | 0.99 |
| P x Litter type | 2 | 48 | 0.99 | 0.38 |
| K x Litter type | 2 | 48 | 0.25 | 0.78 |
| N x P x K | 1 | 21 | 4.00 | 0.06† |
| N x P x Litter type | 2 | 48 | 0.89 | 0.42 |
| N x K x Litter type | 2 | 48 | 0.87 | 0.42 |
| P x K x Litter type | 2 | 48 | 0.12 | 0.89 |
| N x P x K x Litter type | 2 | 48 | 0.16 | 0.85 |
| **HFE** | | | | |
| N | 1 | 12 | 3.43 | 0.09† |
| Irrigation | 1 | 12 | 10.21 | **0.01** |
| Litter type | 2 | 24 | 91.69 | **0.00** |
| N x Irrigation | 1 | 12 | 0.03 | 0.86 |
| N x Litter type | 2 | 24 | 1.29 | 0.29 |
| Irrigation x Litter type | 2 | 24 | 12.44 | **0.00** |
| N x Irrigation x Litter type | 2 | 24 | 0.02 | 0.98 |

Numbers in bold indicate $P < 0.05$. † denotes $P < 0.1$.

**Table 2**
Carbon source and treatment effects on substrate-induced respiration rates at the NutNet and HFE sites.

| NutNet | numDF | denDF | F-value | p-value |
|---|---|---|---|---|
| N | 1 | 21 | 0.13 | 0.72 |
| P | 1 | 21 | 1.25 | 0.28 |
| K | 1 | 21 | 4.00 | 0.06† |
| Carbon source | 6 | 144 | 11.47 | **0.00** |
| N x P | 1 | 21 | 0.25 | 0.62 |
| N x K | 1 | 21 | 2.38 | 0.14 |
| P x K | 1 | 21 | 2.03 | 0.17 |
| N x Carbon source | 6 | 144 | 0.39 | 0.89 |
| P x Carbon source | 6 | 144 | 0.13 | 0.99 |
| K x Carbon source | 6 | 144 | 0.18 | 0.98 |
| N x P x K | 1 | 21 | 0.42 | 0.52 |
| N x P x Carbon source | 6 | 144 | 0.03 | 1.00 |
| N x K x Carbon source | 6 | 144 | 0.21 | 0.97 |
| P x K x Carbon source | 6 | 144 | 0.24 | 0.96 |
| N x P x K x Carbon source | 6 | 144 | 0.12 | 0.99 |
| **HFE** | | | | |
| N | 1 | 12 | 6.12 | **0.03** |
| Irrigation | 1 | 12 | 3.68 | 0.08† |
| Carbon source | 6 | 72 | 36.80 | **0.00** |
| N x Irrigation | 1 | 12 | 1.72 | 0.21 |
| N x Carbon source | 6 | 72 | 1.36 | 0.24 |
| Irrigation x Carbon source | 6 | 72 | 1.60 | 0.16 |
| N x Irrigation x Carbon source | 6 | 72 | 0.78 | 0.59 |

Numbers in bold indicate $P < 0.05$. † denotes $P < 0.1$.

**Table 3**
Treatment effects on nutrient concentration, microbial activity (MicroResp), litter decomposition and microbial abundance at the NutNet and HFE sites.

| NutNet | numDF | denDF | TOC | TON | SIR BT | SIR CEL | SIR GL | SIR GT | SIR LIG | SIR LT | SIR OA | BT deco | GT deco | LT deco | BA | FA | AOB | AOA | F:B |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* | *F* |
| N | 1 | 21 | 0.59 | 0.67 | 0.07 | 0.21 | 1.60 | 2.37 | 0.11 | 1.38 | 0.00 | 0.92 | 0.49 | 0.26 | 0.26 | 0.85 | 0.16 | 0.72 | 0.50 |
| P | 1 | 21 | 1.68 | 1.30 | 0.12 | 0.85 | 2.31 | 0.06 | 0.01 | 0.32 | 0.51 | 0.48 | 0.23 | 1.05 | 1.00 | 0.19 | 0.06 | 0.03 | 0.33 |
| K | 1 | 21 | 0.81 | 0.15 | **4.29** | 3.50 | 0.42 | 0.28 | 2.98 | 3.456† | 0.83 | 0.11 | 0.73 | 1.00 | 1.15 | 0.01 | 0.13 | 0.12 | 1.14 |
| N:P | 1 | 21 | 0.36 | 0.31 | 0.09 | 0.38 | 1.04 | 0.21 | 0.00 | 0.07 | 0.12 | 0.27 | 1.53 | 0.00 | 0.08 | 1.34 | 0.43 | 1.07 | 0.77 |
| N:K | 1 | 21 | 0.20 | 0.26 | 0.27 | 1.41 | 1.17 | 0.03 | 1.70 | 0.18 | **7.55** | 0.50 | 0.00 | 0.84 | 0.24 | 0.09 | 0.25 | 0.20 | 0.06 |
| P:K | 1 | 21 | 0.16 | 0.13 | 0.00 | 4.65† | 0.06 | 0.43 | 0.13 | 1.69 | 1.94 | 0.00 | 0.31 | 0.00 | 0.80 | 1.96 | 0.51 | 1.99 | 0.00 |
| N:P:K | 1 | 21 | 0.01 | 0.53 | 0.07 | 0.13 | 0.08 | 1.18 | 0.24 | 0.98 | 1.08 | 1.21 | 2.73 | 1.55 | 1.17 | 1.07 | 0.59 | 0.00 | 0.87 |
| **HFE** | | | | | | | | | | | | | | | | | | | |
| N | 1 | 12 | 0.03 | **29.37** | 3.63† | 0.01 | 0.00 | 0.01 | **6.13** | 2.84 | 4.10† | 2.34 | 0.06 | **5.47** | 2.91 | 0.95 | 4.53† | 2.62 | 0.09 |
| Irrigation | 1 | 12 | **5.61** | **33.24** | **6.14** | 0.11 | 0.67 | 0.02 | 1.17 | 1.16 | 1.31 | 0.60 | 2.36 | **34.46** | **4.97** | **11.07** | **5.80** | 1.84 | **14.18** |
| N:Irrigation | 1 | 12 | 0.37 | **20.19** | 0.03 | 0.45 | **4.96** | 0.51 | 0.03 | 0.21 | 3.14 | 0.10 | 0.04 | 0.03 | **7.71** | 0.51 | 2.36 | 2.90 | 0.83 |

Numbers in bold indicate $P < 0.05$. † denotes $P < 0.1$. TOC = total dissolved carbon; TON = total dissolved nitrogen; SIR = substrate induced respiration rates; BT = black tea; GT = green tea; LT = local litter; CEL = cellulose; GL = glucose; LIG = lignin; OA = oxalic acid; deco = decomposition (mass loss); BA = bacterial abundance; FA = fungal abundance; AOB = bacterial nitrifiers; AOA = archaeal nitrifiers; F:B = fungi:bacteria ratio.

associated with a greater proportion of AOA (P = 0.07; Table 3). There were no clear changes in total soil extractable C and N associated with nutrient additions at the grassland site (Fig. 2ac; Table 3).

### 3.2. Hawkesbury Forest Experiment (experiment 2)

As was seen for the grassland above, litter quality was the main factor regulating early decomposition rates (i.e., 60 days) at the forest site; green tea was more easily decomposed by the local microbial community than either local litter or black tea (Fig. 1b; Table 1). Irrigation increased litter mass loss during the incubation period (P = 0.006), although this effect was more pronounced in the case of the intermediate (local) and labile (green tea) litters, as evidenced by a significant interaction between irrigation and litter type ($P < 0.001$). Nitrogen addition increased the rate of mass loss of local litter (P = 0.038), but it had no effect on black tea (P = 0.15) or green tea (P = 0.81) litter. Dry N addition consistently reduced SIR rates (Table 2), whereas the addition of N in combination with additional water resulted in SIR levels comparable to the control treatment (Fig. 1d; Table 1). This was particularly evident with the two most labile substrates (glucose and oxalic acid; Table 3). Irrigation also increased oxalic acid-induced (P = 0.07; Table 3), lignin-induced (P = 0.03; Table 3) and black tea-induced (P = 0.08; Table 3) respiration rates. Respiration rates induced by black tea, local litter and, to a lesser extent, green tea showed a pattern very similar to lignin. Irrigation increased bacterial abundance (P = 0.046; Table 3) but reduced fungal abundance (P = 0.006; Table 3), which resulted in a significant shift in the fungi:bacteria ratio (P = 0.003; Table 3). Nitrogen addition alone marginally increased the abundance of bacterial nitrifiers ($P < 0.1$), although there was no effect of N addition in conjunction with irrigation, resulting in a significant interaction between N and irrigation (P = 0.017; Table 3). Irrigation reduced total extractable C, regardless of N addition ($P < 0.001$; Table 3; Fig. 2b). Total extractable N increased with N addition ($P < 0.001$; Table 3), but this was only evident when the N was added in the dry form, as indicated by a significant interaction between N and irrigation ($P < 0.001$; Fig. 2d; Table 3).

### 3.3. Cross-site comparison and system-level understanding about the role of vegetation type, N addition and environmental factors in driving decomposition

Ecosystem type had a stronger influence on early decomposition rates than the experimental manipulations. In this sense, forest soils decomposed litter between 2 and 5 times faster than grassland soils, regardless of the experimental treatments (Fig. 1ab and 3). Substrate-induced respiration rates for labile and intermediate substrates were greater in forest soils compared to grassland soils, whereas the ability to degrade recalcitrant C sources was greater in grasslands (Fig. 1cd and 3). The relative abundance of the four microbial groups was similar at both sites, although overall abundances were consistently greater in grasslands (Fig. 1ef and 3). Total extractable C and N did not vary across ecosystem types, although total N availability and N addition were, after ecosystem type, the second most important drivers of litter decomposition rates, regardless of substrate quality (Figs. 2 and 3). Our SEM also indicated a highly significant negative relationship between the mass loss of local litter and the ability of a given soil to respire oxalic acid and lignin substrates (Fig. 3cd and Fig. S1). In contrast, the ability of any given soil sample to decompose local litter was positively related to its ability to respire C sources of intermediate quality (Fig. 3 and Fig. S1).

## 4. Discussion

Our study indicates that endogenous factors such as ecosystem type, microbial abundance and metabolic capabilities of soil communities

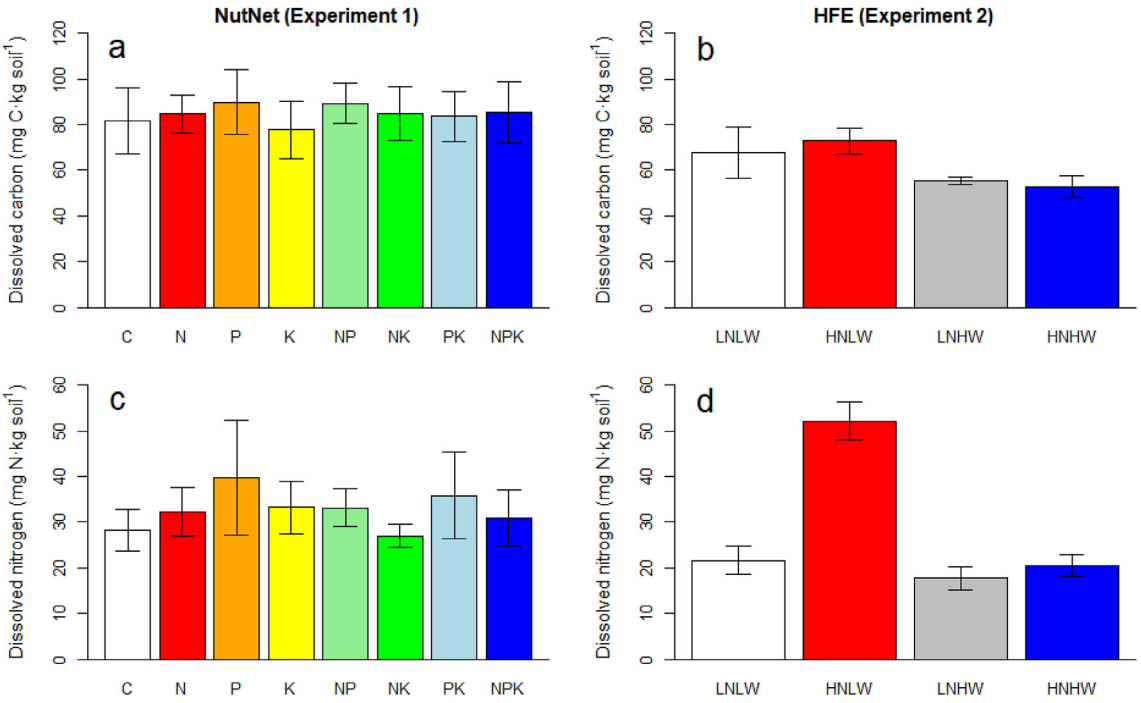


**Fig. 2.** Total dissolved carbon and nitrogen in response to nutrient (NutNet, Experiment 1; left-hand side panels) and N addition plus irrigation (HFE, Experiment 2; right-hand side panels). LNLW = low-N, low-water, HNLW = high-N, low-water, LNHW = low-N, high-water, HNHW = high-N, high-water.

may be more important than nutrient inputs and irrigation (as representative of global change drivers) in regulating litter decomposition rates in managed grassland and forest ecosystems in Australia. In particular, our study suggests a clear hierarchy of factors driving the early litter decomposition processes at the local scale. This hierarchy is, in decreasing order of importance, (1) ecosystem type, including differences in N availability and in the abundance of the microbial communities found therein, (2) litter quality, and (3) the direct effects of nutrient and/or water addition. These results are key to contextualize the importance of different global change drivers in regulating decomposition rates, and ultimately suggest that conversions from forest to grasslands can have a much larger effect on litter decomposition than other global change drivers such as fertilization or altered rainfall regimes.

### 4.1. Ecosystem type

Ecosystem type (here grassland vs. forest) and the structure and composition of plant communities are well known drivers of decomposition processes at the global scale (Zhang et al., 2008). Forested ecosystems typically show greater rates of decomposition compared to non-forested ecosystems (Zhang et al., 2008). In agreement with this general pattern, the eucalypt forest (Experiment 1) underwent more rapid initial stages of decomposition compared to the grassland site, a result that was most likely driven by the metabolic capabilities of the soil microbial communities present at each site (Cleveland et al., 2014; McGuire and Treseder, 2010). In this sense, our SEM analysis suggests that bacterial abundance plays a particularly important role in the metabolic abilities of soils; however, we did not measure community composition or richness, which may account for the relatively modest relationships found between microbial abundance and both substrate-induced respiration and decomposition rates. These variables (i.e., microbial community composition and richness) may have, in turn, been captured in our classification of ecosystem type, hence the importance of the latter as a predictor of decomposition rates (McGuire and Treseder, 2010).

### 4.2. Litter and substrate quality

The second factor in the hierarchy controlling litter decomposition was litter quality, which consistently accounted for differences in mass loss of up to 15% at both sites. At both sites, green tea, the most labile substrate, decomposed faster, and glucose and oxalic acid were consistently the two substrates more easily respired in the laboratory assay. This is in agreement with a recent global study in which green tea litter bags (labile substrate) decomposed significantly faster than rooibos litter bags (recalcitrant source) during a 90-day field incubation (Djukic et al., 2018). Our results indicate that, despite clear innate differences between the two sites in terms of their ability to decompose litter regardless of its quality, future changes in litter quality due to alterations in the biomass and composition of plant communities in response to human impacts (Dijkstra et al., 2012; Djukic et al., 2018) can have significant implications in terms of ecosystem functioning through the way in which microbial communities process organic matter inputs (Garcia-Palacios et al., 2013).

### 4.3. Nutrient addition and irrigation

Finally, the experimental treatments, considered as proxies of global environmental change drivers (that is, increases in precipitation that are predicted for some regions of the world and eutrophication (Fowler et al., 2013; IPCC, 2014)), accounted for differences in our measured variables that ranged from 10 to 15% in the case of the irrigation plus N addition treatment at the HFE (Experiment 2) to almost negligible in the case of most of the nutrients (and combinations of nutrients) added in Experiment 1. In the SEM, only the ability to respire recalcitrant C was globally downregulated by N addition, which is agreement with results from a global meta-analysis in which N addition was demonstrated to downregulate the decomposition of recalcitrant litter (Knorr et al., 2005).

Nitrogen fertilization typically reduces microbial biomass and soil respiration rates (Treseder, 2008), which could plausibly account for reductions in litter decomposition rates and enhanced C sequestration observed in forest ecosystems due to accumulation of undecomposed

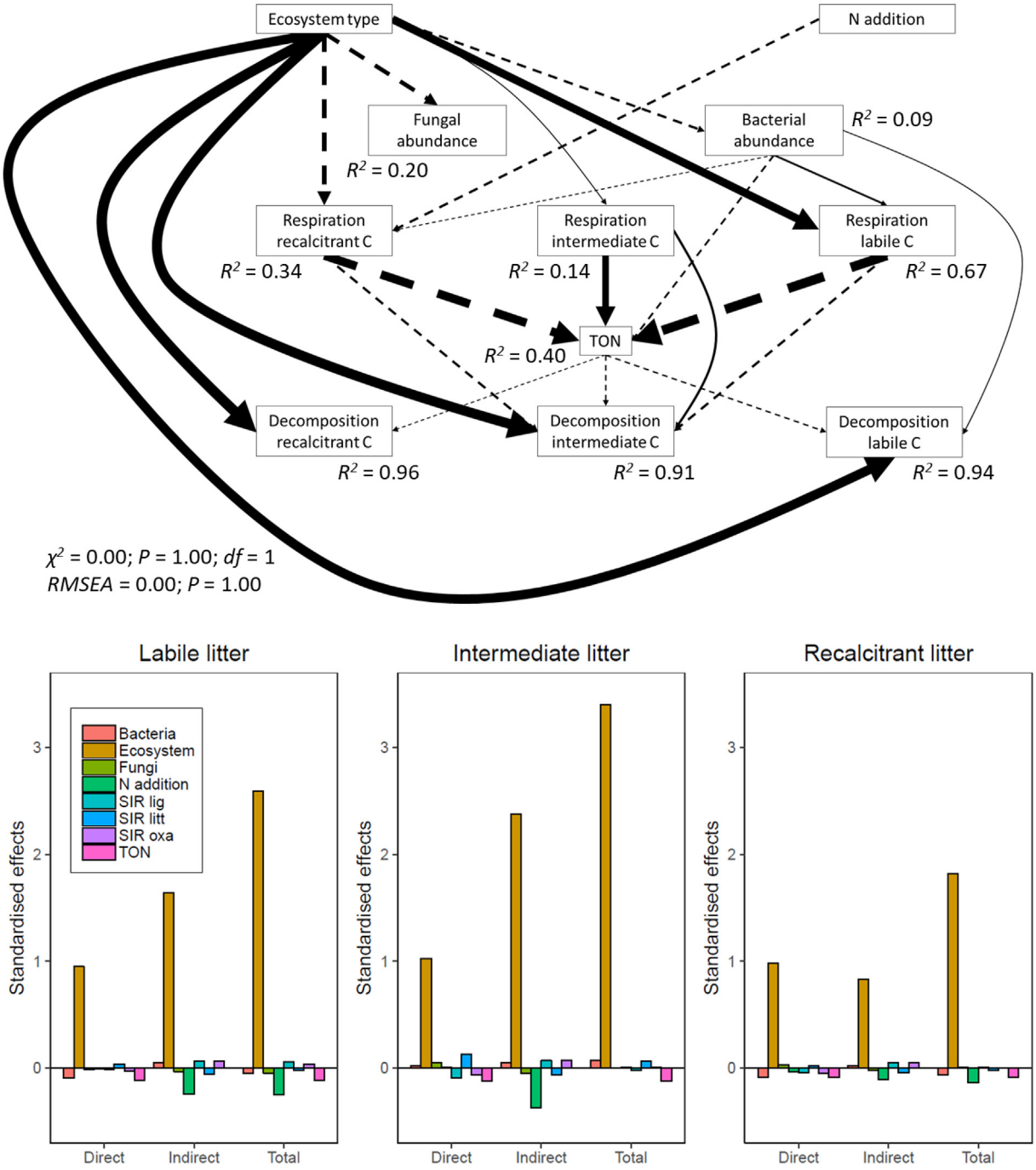


**Fig. 3.** Structural equation model depicting hypothesized causal relationships between ecosystem type (forest = 1, grassland = 0), N addition (control = 0, N added = 1), microbial abundance, the ability of microbial communities to respire C-based substrates, and N availability on litter decomposition for the three different substrates (top panel). The three bottom panels represent the standardised direct, indirect and total (i.e., direct + indirect) effects of global change and environmental drivers on the decomposition of labile (green tea), intermediate (local plant material) and recalcitrant (black tea) litter. TON = total organic N. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

plant litter (Maaroufi et al., 2015). This is thought to be particularly true in ecosystems where recalcitrant litter inputs dominate (Knorr et al., 2005). In partial agreement with these studies, our N addition treatment significantly reduced the ability of soil microbes to respire organic substrates at the HFE site, while water addition returned values to almost control levels. This suggests that microbial functioning might be particularly impaired under N deposition in dry environments, which could be due to toxic effects of excessive N (Ochoa-Hueso et al., 2017, 2016). A similar mechanism has already been suggested for the way in which plant communities respond to N in seasonally water-limited environments (Ochoa-Hueso et al., 2011). The lack of an effect of N addition on microbial respiration at the grassland site contrasts with our findings at the forested site and, beyond mechanistic reasons, this may reflect the fact that the grassland had only been fertilized once by the time this study was carried out, compared to seven years of treatment in the case of the forested site. Despite the lack of N effects, the significant effect of K addition (plus micronutrients) on the ability of microbes to degrade organic matter in the grassland points to the role of other often overlooked nutrients, such as K, for organic matter processing dynamics (Sardans and Peñuelas, 2015). Supporting the role of

K for ecosystem functioning, a recent coordinated study involving over forty experimental sites within the Nutrient Network demonstrated that productivity in global grasslands is very often limited/co-limited by K (Fay et al., 2015). Similarly, micronutrients such as Mn are known to be relevant drivers of litter decomposition at the global scale and also to limit the response of litter decomposition to N deposition (Keiluweit et al., 2015; Whalen et al., 2018), supporting our results.

### 4.4. Conclusions

Taken together our results suggest that, at least at local scales, drastic land use conversions and intrinsic factors associated with each ecosystem type, including litter quality, may be more important than global change drivers that result in changes in N and water availability in controlling litter decomposition. This highlights the importance of identifying the role of land use and plant community change in C cycling and associated terrestrial feedbacks under future global change scenarios. Our study also identifies the potential role of soil nutrients other than N and P that are frequently overlooked (K, in this study) in controlling litter decomposition, and therefore C cycling and sequestration rates. Finally, we suggest the importance of considering fine-resolution microbial community attributes that may underlie ecosystem-specific responses of litter decomposition to global change (McGuire and Treseder, 2010).

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2018.11.009.

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